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Leaf Growth Rates (*Thalassia testudinum*, Banks ex Koning) as an Indicator of Seagrass Responses to Freshwater Releases

Eric C. Milbrandt and Jeff Siwicke

In southwest Florida, changes in hydrology have fundamentally changed the timing and amount of freshwater delivered to the estuarine ecosystem. Biological indicators such as oyster and submerged aquatic vegetation distribution and abundance have been used to establish minimum and maximum discharges to the estuary. These indicators are robust long-term indicators for comparing interannual and climatological changes; however, they lack sensitivity to variable freshwater flows that occur over the course of months or seasons. Seagrass leaf growth rates could provide an integrated biological response for evaluating events caused by climatological shifts (e.g., El Niño) or to evaluate the biological responses to management actions (e.g., flood control releases of freshwater from Lake Okeechobee). Leaf growth rates for *Thalassia testudinum* were determined monthly across a gradient of increasing distance from the mouth of the Caloosahatchee estuary. Leaf growth at sites near the Caloosahatchee (within 5 km) had significantly lower growth rates during the April–June period. Salinity was also significantly lower, while light attenuation and temperature were not significantly different. High discharges for flood control caused lower salinities and significantly slowed leaf growth rates. Leaf growth can be a sensitive indicator to water management and climatological events and can show an integrated biological response to high flows.

Introduction

The management of freshwater inflows to an estuary can have profound effects on estuarine ecosystem function (Alber, 2002; Kimmel and Roman, 2004). Increasing worldwide demands for freshwater use and the loss of critical habitats in coastal areas (Short and Wyllie-Echeverria, 1996; Lotze et al., 2006) are contributing to the need for prioritization, allocation, and delivery of freshwater to coastal systems (Montagna et al., 2002). Similar to many urbanized coastal areas, south Florida estuaries have been significantly altered over time, and the timing and delivery of freshwater to the estuaries are highly managed.

The Caloosahatchee watershed is approximately 362 kha, with primarily agricultural and urban land uses. The Caloosahatchee Estuary is connected to Lake Okeechobee through a system of lift gates and levees (S-77, S-78, S-79) to control flow volumes (Lake Okeechobee Waterway, U.S. Army Corps of Engineers). When connected to the lake, the watershed is artificially expanded to 1,500 kha. The schedule for releasing water from Lake Okeechobee to the Gulf of Mexico (Cadavid et al., 2006) is dependent on climatological predictions and the stage of Lake Okeechobee. When the level exceeds a certain threshold, pulsed discharges or continuous discharges to the estuary and coastal waters are made. Additionally, freshwater flows from the Caloosahatchee River (C-43 canal) watershed driven by rainfall and water storage and allocations enter the estuary at structure S-79. This highly modified water storage and conveyance system results in extreme low and extreme high flows, which have caused widespread habitat losses in the Caloosahatchee Estuary.

Along with the loss of shoreline habitat and function, the draining and channelization of water for the purposes of agriculture and diversion of water for urban development have led to increased wet season flows and decreased dry season flows (Doering and Chamberlain, 1999). This has resulted in losses of submerged aquatic vegetation because of saltwater intrusion (Orlando and Douglass, 2014) during droughts. Conversely, consecutive years of above-average rainfall, high flows, and flooding have resulted in decreases in spat settlement (Wilson et al., 2005). Additionally, high nutrient loading from an agricultural and urbanized watershed has led to large-scale macroalgae stranding events (Dawes, 2004; Lapointe and Bedford, 2007) and cyanobacterial blooms (Paerl et al., 2008).

Seagrasses provide a wealth of ecosystem services worth as much as $3,500 ha/yr, including support of subsidence fisheries (Watson et al., 1993; de la Torre-Castro et al., 2004), nutrient cycling (de la Torro and Ronnback, 2004; McGlathery et al., 2007), sediment stabilization (Romero et al., 2006), and sequestration of carbon (Duarte et al., 2005; Orth et al., 2006).

The number of sites reporting losses of seagrasses has increased every decade, and total aerial losses are estimated at 2,000–3,000 km^2 per decade globally (Short and Wyllie-Echeverria, 1996; Waycott et al., 2009).

Low salinity and low light availability from freshwater discharges threaten seagrass species distribution and abundance (McPherson and Miller, 1994; Kraemer et al., 1999; Greenawalt-Boswell et al., 2006). Salinities of less than 20 and light attenuation of greater than 1.5/m from freshwater discharges in 2005 were among the drivers of widespread decreases in percent cover and biomass of *Syringodium filiforme* in the Indian River Lagoon (Buzelli et al., 2012). There was a 1-yr lag in the declines, suggesting that identification of a more sensitive metric to indicate plant health would be useful for adaptive management of freshwater flows. The use of habitat suitability models for *Thalassia testudinum* suggested that higher, more stable salinities were a key factor (Santos et al., 2012). When subjected to rapid declines in salinity, *T. testudinum* showed a sudden stress reaction, prompting an increase in the amount of dead tissue and defoliation (Chollett, 2007). Percent cover, shoot density, and biomass of seagrasses declined precipitously when weekly salinities ranged from 13.5 to 19.8 ppt, with salinities caused by high rainfall and freshwater inputs to the Indian River Lagoon (Hanisak, 2002). Instantaneous productivity measurements using PAM fluorometry showed a decrease in photosynthetic performance in *T. testudinum* seedlings, at salinities below 30 (Kahn and Durako, 2006).

The amount of available light appears to drive the photosynthetic production to support growth and responses to stressors (Hemminga and Duarte, 2000). Globally, seagrasses require up to 36% subsurface irradiation (Dennison et al., 1993). Numerous studies have found negative correlations between seagrass depth range and light attenuation (Goldsborough and Kemp, 1988; Abal and Dennison, 1996). As flows increase, nutrient loading increases, which can result in decreased light availability (Moore and Wetzel, 2000). Phytoplankton biomass, turbidity, and colored dissolved organic matter affect the available light to seagrass by increasing scattering and absorption in the water column (Biber et al., 2009).

Thalassia testudinum is a climax species with high light requirements, and the species lives in the lower estuary. Sublethal effects of prolonged low salinity and low light availability can be measured using marking techniques developed in the early 1970s (Zieman, 1975). Leaf marking methods were used to determine the net leaf production of seagrass (Dennison, 1990) as an integration of the gross production minus respiratory and excretory losses. Short (1987) used leaf marking to determine the length of new leaf tissue and converted to leaf weight with a length-to-weight relationship as a nondestructive method for determining biomass production. Many seagrass growth studies have focused on species with flat blades, such as *Thalassia*. Durako (1994) applied this method to elucidate the population dynamics of three populations in Florida Bay.

Table 1. Sites at which leaf growth rates were collected from Dec. 2005 to Oct. 2008. Site names are provided with the distance to the Sanibel causeway, latitude, longitude, sample depth. and sample size.

Site	Distance (km)	Latitude	Longitude	Depth (m)	n
S8	1.59	26.50937 N	−82.04432 W	1.5	540
CW	1.14	26.49810 N	−82.01751 W	1.5	536
MW	3.01	26.48357 N	−82.01056 W	1.5	611
TL	0.68	26.47836 N	−82.02574 W	1.7	415
WP	5.10	26.46888 N	−82.05756 W	2.0	498
TB	7.99	26.45783 N	−82.08643 W	2.0	536
RF	13.20	26.48415 N	−82.14769 W	2.2	489

In the Caloosahatchee Estuary, high-volume discharges into the estuary are predicted and are routine occurrences, and, therefore, there is a growing need to understand sublethal responses (Volety et al., 2009) by select indicator species. There are large areas in the lower estuary that are affected by seasonal freshwater flows from S-79. In this 3-yr study, we determined the effects of light availability and salinity on *T. testudinum* leaf growth at shallow-water sites (Table 1) at varying distances from the mouth of the Caloosahatchee. The goal was to understand how regulated and climatological freshwater inputs would affect seagrass growth over several growing seasons.

Materials and Methods

Flow.—Daily flows for water control structure S-79 were collected by the U.S. Army Core of Engineers, Jacksonville District (http://www.saj.usace.army.mil/h2o/reports/r-s79m.html). The flows from S-79 represent a majority of flow to the estuary (minus the tidal basin). Flows were reported in centimeters (cubic meters per second).

Physical parameters.—Salinity, temperature, and dissolved oxygen were measured using a Hydrolab Quanta sonde with a hand-held display (OTT Hydromet, Kempten, Germany). Calibrations of salinity and dissolved oxygen were performed monthly prior to sample collection following the manufacturer's protocols. Downwelling irradiance was measured with paired Biospherical (San Diego,

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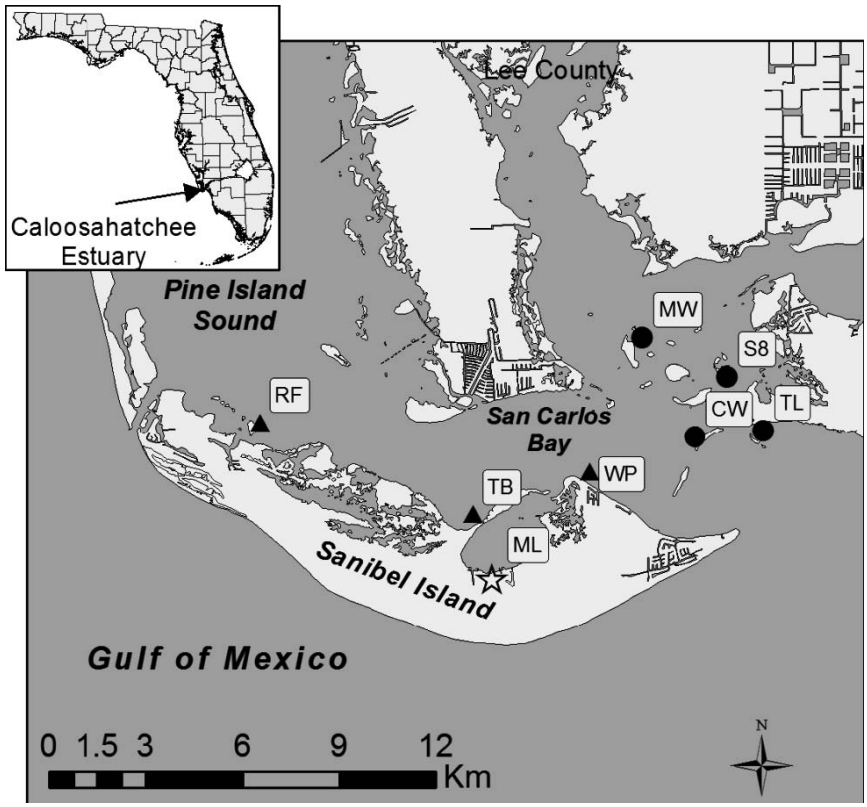

Fig. 1. Map of the study area. *Thalassia testudinum* leaf growth rates were measured from Jan. 2005 through Dec. 2008. Locations represented with a triangle are greater than 5 km from the mouth of the Caloosahatchee, while circles are locations less than 5 km from the mouth. The location of the Sanibel Captiva Conservation Foundation (SCCF) Marine Laboratory is indicated with a star and ML.

CA) BIC loggers, recording at 1-sec intervals for 30 sec. These 2π multichannel radiometers recorded irradiance in the following channels: 433–453 nm (blue), 465–485 nm (blue–green), 500–520 nm (green) and 400-700 nm PAR (photosynthetically active radiation). The instruments were offset by 1 m and were deployed for 30 sec from small boats or in some cases from docks. Irradiance data were used to calculate light attenuation coefficients for the four channels according to Beer's law, as follows:

$$K_d = \ln(I_1/I_2)/(Z_2\text{-}Z_1), \quad (1)$$

where K_d is light attenuation coefficient and I_1 and I_2 are downwelling irradiances at depths at Z_1 and Z_2, respectively. Calculations of K_d for four spectral bands, blue, blue–green, green, and PAR, were performed using Equation 1.

Leaf marking and growth.—A map of the study area indicates the sampling sites in the Caloosahatchee Estuary, San Carlos Bay, and Pine Island Sound (Fig. 1). Leaf growth rates (Kraemer et al., 1999; Kraemer and Hanisak, 2000) were measured in field-incubated individuals (Zieman, 1975) in the study area (Fig. 1, inset). Six individual *T. testudinum* shoots were marked at the base of the shoot with an 18-gauge syringe needle at each site. After 2–4 wk, the whole shoot was harvested and brought back to the lab in plastic baggies filled with ambient estuary water and measured on the same day. Blade length, blade width, and the number of blades per shoot were determined (Short and Coles, 2001) for a total of 42 shoots. Growth rates were determined from the growth of each leaf from the base of the shoot to the leaf scar created by the syringe needle.

Growth rates were determined by measuring the distance from the leaf scar on the growing leaf and comparing to the leaf scar on an older, nongrowing leaf. The number of leaves per shoot varied, so the average growth rates of all leaves were averaged. Leaves were dried at 60°C to constant weight to determine a locally

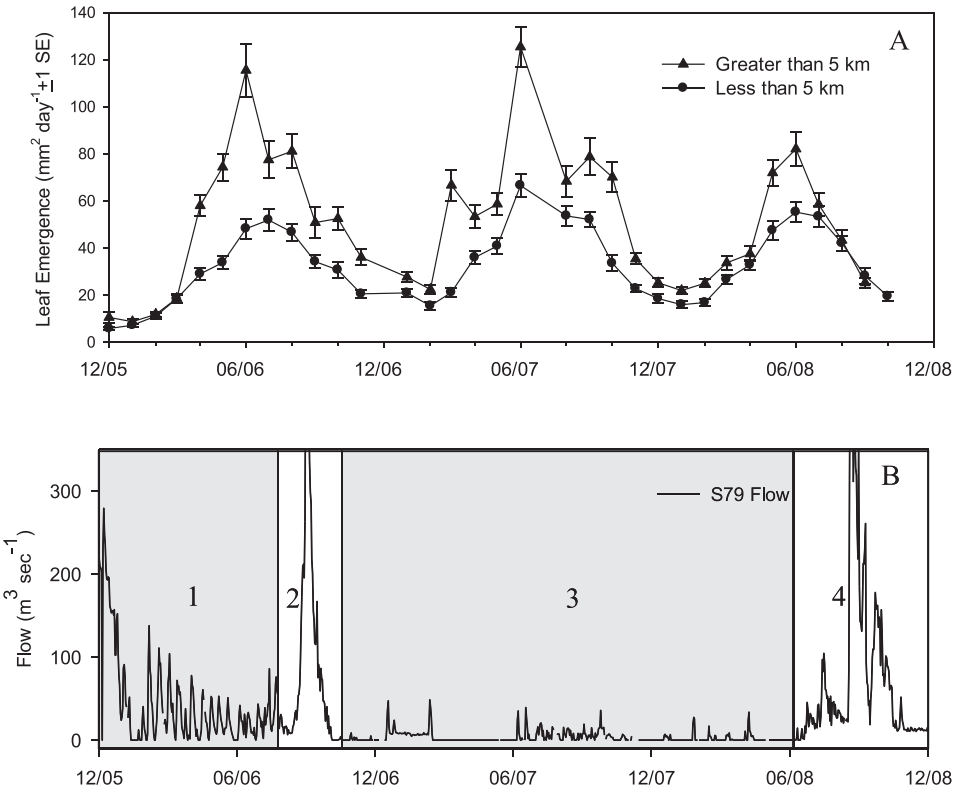

Fig. 2. (A) Leaf growth grouped by distance from the Caloosahatchee. (B) Flow from S-79 (A) and *Thalassia testudinum* leaf growth measured from Dec. 2005 to Nov. 2008. Flow data from S-79 were obtained from USACOE, Jacksonville District. Four discharge periods are described: (1) high-volume pulsed discharges during the dry season to lower Lake Okeechobee, (2) high discharges associated with Tropical Storm Ernesto, (3) low discharges due to a drought, and (4) high discharges associated with Tropical Storm Fay.

calibrated relationship between leaf area and dry weight (Pearson, n = 48, R^2 = 0.96) for determining net areal leaf production. Seagrass growth per blade was calculated by multiplying blade widths by the distance between the leaf scar on the younger blade to determine the area added (growth).

Sites were grouped for analysis based on the distance from the mouth of the Caloosahatchee River (the major freshwater source of freshwater). Sites situated less than 5 km away were grouped together (CW, MW, TL, S8), and those situated greater than 5 km away were grouped (TB, TL, RF) for statistical analysis. Leaf growth data were arcsine transformed in Excel, then imported into Minitab (version 13). The regions were first tested for homoscedasticity with a Levene's test and for normally distributed data with a Kolmogorov–Smirnov test. A General Linear Model (GLM) was used with growth as the dependent factor and the date harvested and region as independent factors. Post hoc tests on a fully factorial model were completed with Tukey pairwise comparisons. All physical data were also tested for equal variances (Levene's test) and normal distribution (Kolmogorov–Smirnov test) and imported into Minitab (version 13). A GLM was used with date harvested and region as independent factors and with the physical parameters as dependent factors. Monthly mean growth between regions was correlated with monthly mean temperatures and mean salinities (Pearson; Minitab).

Results

Freshwater flows from S-79 were obtained from the U.S. Army Corps of Engineers, Jacksonville District, and daily flows were plotted over the period of study. Based on the hydrograph there were four notable periods (Fig. 2B). The first was a period of pulsed discharges during the dry season (Nov. through May; South Florida Water Management District, 2009) from Dec. 2005 until June 2006. This was followed by a wet period and high discharges associated with tropical storm activity (Jul. 2006–Nov. 2006). Starting in Nov. 2006 there was a drought,

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TABLE 2. General Linear Model results of salinity. Salinity was the dependent value, with region and month serving as independent variables.

Source	DF	Seq SS	Adjusted SS	Adjusted MS	F	*P*
Region	1	102.98	96.33	96.33	32.42	0.000
Month	30	5,983.77	5,718.34	190.61	64.16	0.001
Region*Month	30	198.42	198.42	6.61	2.23	0.001
Error	155	460.5	460.5	2.97		
Total	216	6,745.68				

Seq SS - Sequential sums of squares, MS - Mean Square.

and discharges until June 2008 were well below average levels. At the beginning of the wet season in 2008, large wet season flows resumed.

Salinities were significantly higher at sites located greater than 5 km from the mouth of the Caloosahatchee River (Region; Table 2) and, therefore, significantly lower at sites located less than 5 km from the mouth of the river. There were significantly lower salinities in 2006 and 2008 (July–Sep.) at all sites in which salinity was a significant factor (Month; $F = 2.23$; $P < 0.001$). Significantly lower salinity at sites located less than 5 km from the Caloosahatchee were found in Aug. (t-value, −5.30) and Sep. (t-value, −4.210) 2006. In 2007, there were no differences between regions. However, in 2008, with the return of high summer flows, salinity was significantly lower at sites near the Caloosahatchee in Sep. (t-value, −4.38).

There were significantly higher leaf growth rates at sites that were situated greater than 5 km from the mouth of the Caloosahatchee River than at sites situated less than 5 km away (Fig. 2A; Table 3; Region; $F = 217$; $P < 0.000$). There were also significantly lower salinities in 2006 and 2008 (July−Sep.) at all sites, and it was a significant factor in the GLM (Table 2; Month; $F = 2.23$; $P < 0.001$).

While the regional differences in salinity were significant, the differences in salinities between regions were not as large as the regional differences in leaf growth (Figs. 2, 3), as reflected in the F-values of the GLM. The greatest F-value was from the regional comparison of leaf growth (Table 3). There were significant differences in leaf growth at sites separated by distance from the Caloosahatchee (region) for most months, as indicated by the interaction term of the GLM (Region*Month). A pairwise comparison by region and month indicated significantly higher leaf growth at distances greater than 5 km from the Caloosahatchee (Bonferroni, Minitab). In 2006, significantly lower leaf growth was found for seagrass near the Caloosahatchee from April through June (t-values, −4.90, −6.68, and −6.19, respectively). In 2007, significantly lower leaf growth was measured near the Caloosahatchee in March, June, and Oct. (t-values, −8.06, −4.32, and −4.58, respectively). Significant differences were not detected in 2008.

Despite being in a subtropical climate at 26°N latitude, there was a significant seasonal effect, as reflected in significant differences in leaf growth between months (Table 3; Month; $F = 40.18$; $P < 0.000$).The highest leaf growth rates were measured during maximum day length from May to July, with June having the highest rates in all years. At sites greater than 5 km from the Sanibel Island causeway bridge, (RF, TB, and WP) peak growth rates were 115 mm^2/d in June 2006, 125 mm^2/d in June 2007, and 82 mm^2/d in June 2008. Peak growth rates at sites less than 5 km from the Sanibel causeway (TL, TB, S8, and MW) occurred in July 2006 (52 mm^2/d), June 2007 (67 mm^2/d), and June 2008 (55 mm^2/d). Minimum growth rates occurred from Nov. through March, corresponding to shorter day lengths and lower temperatures. There was a significant positive

TABLE 3. General Linear Model results of leaf growth. Data were arcsine transformed before to meet equal variance and normal distribution requirements. Salinity was the dependent value, with region and month serving as independent variables.

Source	DF	Seq SS	Adjusted SS	Adjusted MS	F	*P*
Region	1	137.353	125.296	125.296	217	0.000
Month	32	745.957	739.193	23.1	40.18	0.000
Region*Month	32	54.569	54.569	1.705	2.97	0.000
Error	2,743	1,577.134	1,577.134	0.575		
Total	2,808	2,515.013				

Seq SS - Sequential sums of squares, MS - Mean Square.

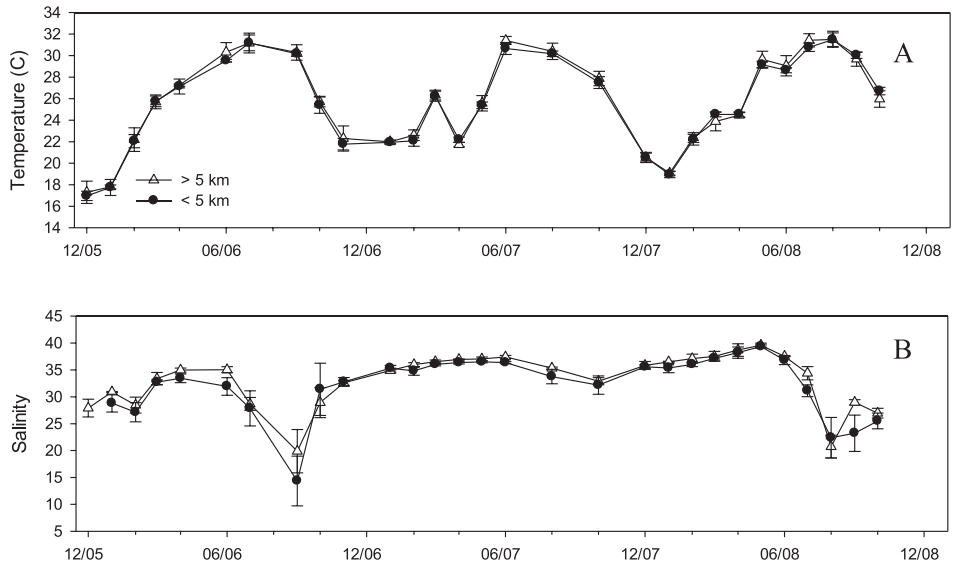

Fig. 3. Mean temperature and salinity separated by region from Dec. 2005 to Nov 2008.

correlation between leaf growth and temperature for all sites (Pearson, 0.691). Other correlations between leaf growth and salinity (Pearson, 0.222), light attenuation (Pearson, 0.005), and blue light attenuation (Pearson, 0.005) were not significant.

Discussion

There are few studies that measure *T. testudinum* leaf growth in consecutive months for a 3-yr period. Because of the 3-yr study duration, factors such as rainfall and climate could be compared between years. Consistently lower mean leaf growth rates were found at sites located less than 5 km from the mouth of the Caloosahatchee River than were noted at sites located greater than 5 km from the river mouth. The salinity at the sites near the Caloosahatchee was highly variable within a typical growth year for *Thalassia*, while sites further away had more stable salinities. Predictive models of *Thalassia* routinely predict that productivity and biomass are greater where salinities are more stable (Fong and Harwell, 1994; Lirman and Cropper, 2003). Other seagrass metrics, such as biomass and shoot growth rates, are also greater where salinity is more stable (Irlandi et al., 2002; Lirman and Cropper, 2003). Other studies of *T. testudinum* in Florida Bay indicate lower growth rates coincident with lower salinity (Zieman, 1999).

The effects of periodic high freshwater flows on seagrass have been studied elsewhere in South Florida (Tomasko et al., 2005; Irlandi, 2006). Field studies indicate that there is a significant relationship between *T. testudinum* productivity and salinity (Tomasko and Hall, 1999). The results of this study support previous findings but also suggest that leaf growth may be more affected by low salinities during the early part of the annual growth period (April–June) than later in the annual growth period (e.g., during the wet season). During typical wet season high flows the differences in leaf growth were not significant. Mean leaf growth was lower at sites near the source of freshwater, the Caloosahatchee, overall because of lower salinities. Lower light availability caused by higher light attenuation was hypothesized to also affect leaf growth; however, light attenuation coefficients in the PAR spectrum and in the blue spectrum (433–453 nm) were not significantly correlated to leaf growth. Similar to other instantaneous physical parameters that were measured, the light field on the day during which seagrass was harvested was not representative of the time-integrated response of leaf growth. The effect of light on biomass and growth of seagrasses is integrative, as described previously (Dennison and Alberte, 1985; Carter et al., 2000).

Temperature was not significantly different among regions during the study; however, it did have a strong influence on leaf growth rate, as demonstrated by the significant positive correlation. Tomasko and Hall (1999) demonstrated the confounding effects of temperature and freshwater flows in Charlotte Harbor. In this study, temperature and leaf growth were confounded because of the seasonality associated with day length, and longer days occur during the wet season, with higher freshwater flows resulting

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in greater leaf area, shelf-shading, and variability in growth rates (Zimmerman, 2003).

Other studies of *T. testudinum* in Florida Bay have shown lower growth rates coincident with lower salinity (Zieman, 1999). Until the improvements in water storage expected with Everglades restoration occur (Sklar et al., 2005), wet season freshwater flows will lower productivity of seagrasses near the mouth of the Caloosahatchee and near the Sanibel causeway. However, additional research on the factors that drive leaf growth is still needed (e.g., available belowground reserves, epiphyte cover, burial by macroalgae, physical disturbance, resuspension grazing by fish).

The relationship between floodwater releases and leaf growth is especially relevant in Florida, where seagrass habitats are threatened by the prospect of increased rainfall associated with climate change and by water releases associated with flooding. The expansive seagrass habitats near the mouth of the Caloosahatchee Estuary are threatened by the operations of water control structures, which can add 50% of freshwater flows (and associated nonpoint source runoff) from outside of the historic watershed (South Florida Water Management District, 2009). The operations are optimized for flood control and water storage benefits by upstream users, which threaten downstream estuarine ecosystems.

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